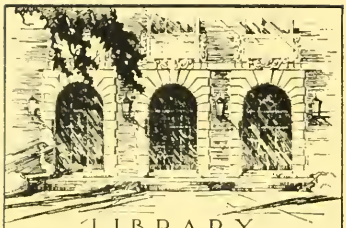

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UPPER PREMOLAR-MOLAR STRUCTURE IN THE NOTOUNGULATA WITH NOTES ON TAXONOMY

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Results of the First Marshall Field Paleontological Expedition to Argentina and Bolivia, 1922–24

Among the large series of notoungulates from the Deseado and Colhué-Huapí formations of Patagonia, collected by the Scarritt Patagonian Expedition of the American Museum (1930–31) and the First Marshall Field Expedition (1922–24), are a number of specimens showing unworn or little worn premolars and molars, and a few with milk molars remaining. Several new characters are revealed by these specimens. The transition from premolars to molars is usually abrupt in members of this order but most of the crown elements, with the possible exception of the protocone, seem to be homologous in both series.

A great deal has been written on the notoungulate dentition, particularly by Ameghino, Gaudry, Scott, and Roth, but nevertheless a general review written in the tritubercular nomenclature seems desirable at this time, even though much remains to be learned.

In this paper a representative genus of each family is described, wherever practicable,[1] and a brief summary is given in conclusion. The notes and figures on *Notostylops* and *Pleurostylodon* have been extracted from a paper written by Mr. E. S. Riggs and myself, which has been in press for some three years. The lower dentition is not discussed here. The structure of the lower premolars and molars is remarkably uniform throughout the order; a complete account of the general structure and of the molarification of the premolars of one genus therefore practically suffices for all. Such an account (of *Notopithecus*) is given in the paper just mentioned.

[1] The Henricosborniidae of the Notioprogonia and the doubtfully typotherian Archaeohyracidae and Acoelodidae are not included.

The drawings, except figs. 17 and 21, which are by Mr. Sydney Prentice, are the work of Mr. Carl F. Gronemann, Staff Illustrator of Field Museum. I am indebted to Professor W. K. Gregory for critical suggestions on the homologies of the lingual cusps, and to Dr. Walter Granger for the information contained in the footnote on page 107.

Order NOTOUNGULATA Roth

In all the members of this order there is a marked tendency to develop cuspules on the floor of the central valley and on the internal slopes of the ectoloph and metaloph.[1] An antecrochet on the protoloph occurs in some cases. This tendency may be regarded as an ordinal character. The distinctions between the upper cheek-teeth of the various families are due largely to the patterns assumed by these cuspules.

Suborder TOXODONTA Owen. LEONTINIIDAE Ameghino

Leontinia Ameghino. Fig. 10.

Specimens of this genus from the Deseado beds at Cabeza Blanca show the development of the premolars in a very satisfactory manner. P^1 has a strongly sinuous ectoloph with a prominent parastyle, separated by a deep groove from the stout parametacone, and a small metastyle. The external cingulum is very well developed and extends downward to the parastyle and metastyle. The large protocone is connected by two high cingula to the parastyle and to the center of the posterior face of the tooth. Several small cuspules are present on the internal slope of the parametacone and on the external slope of the protocone. There is a prominent postero-median cuspule (metaconule) which has become joined to the ectoloph.

On P^{2-4} the external cingulum becomes progressively weaker and the groove between parastyle and paracone becomes shallower. The paracone and metacone are distinct. On P^2 the metaconule joins the ectoloph to the protocone, forming the metaloph. Small ridges of enamel tend to join the external half of the anterior cingulum to the protocone. On P^3, P^4 this tendency is carried to completion

[1] The terms protoloph, metaloph, crista, and crochet, as used in this paper, are employed solely as topographical names without implying developments homologous to those observed in other orders. The term protocone is used for the main internal cusp on the premolars and milk molars although the possibility is recognized (Gregory, 1934) that it may not be homologous to the protocone of the molars.

and the protoloph formed. The lingual slope of the protocone is grooved, the groove becoming progressively deeper on P^{2-4}.

The molars are distinguished chiefly by their greater antero-posterior diameter (when little worn) and by the division of the lingual face, a feature which is foreshadowed in the premolars by

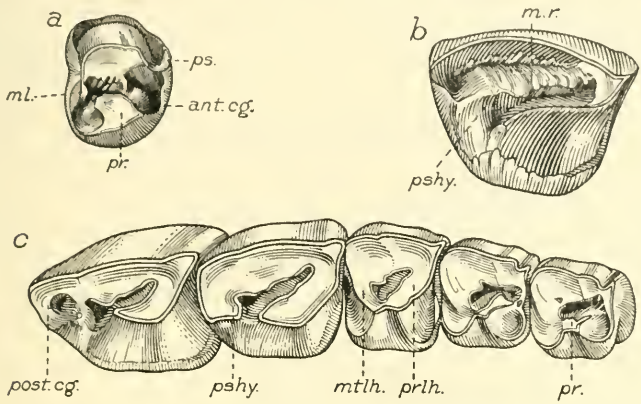

FIG. 10. *a*, *Leontinia gaudryi* Ameghino. P^1, F.M. No. P14659. x 1/1. *b*, *Leontinia gaudryi* Ameghino. M^1, F.M. No. P14659. x 2/3. *c*, *Leontinia* sp. P^2–M^3, F.M. No. P13386. x 2/3. *ant.cg.*, anterior cingulum; *m.r.*, median ridge; *ml.*, metaconule; *mtlh.*, metaloph; *post.cg.*, posterior cingulum; *pr.*, protocone; *prlh.*, protoloph; *ps.*, parastyle; *pshy.*, pseudohypocone.

the lingual grooves on the protocones of P^{2-4}. The division is not apparent on M^3. The postero-internal cusp, to which the term pseudohypocone (Gregory, 1920, p. 149) may properly be applied,[1] probably developed in conjunction with the upgrowth of the entoconid (posterior pillar of some authors) on the lower molars of the ancestral forms. On the molars the anterior cingulum loses its connection with the anterior slope of the protoloph and is relegated to the base of the crown. The posterior cingulum, however, retains its connection with the posterior slope of the pseudohypocone. As a result of the prolongation of the ectoloph posterior to the metaloph this cingulum becomes enlarged, enclosing, with the metaloph, a posterior fossette.

The pattern of unworn molars, hitherto unrecorded, is revealed by specimens at hand. The most striking feature is the presence of a massive, papillate ridge in the central valley which runs from the center of the metaloph to the paracone. This ridge has strongly serrated sides and was undoubtedly formed by the coalescence of cuspules originating on the floor of the valley. The groove separating

[1] See page 106 for the probable developmental relationships of the protoloph and pseudohypocone of the molars.

ridge and ectoloph is shallow and the two become united very early in the wear of the tooth. The impression received from a worn tooth is that the ectoloph is very broad and the central valley narrow. A few cuspules are situated in the groove mentioned above, others form minute vertical ridges on the internal slope of the ectoloph.

On P^{2-4} of *Leontinia* the anterior cingulum remains attached to the anterior slope of the protoloph. Premolars of *Ancylocoelus* and *Colpodon* (fig. 11) illustrate the encircling of the protoloph by

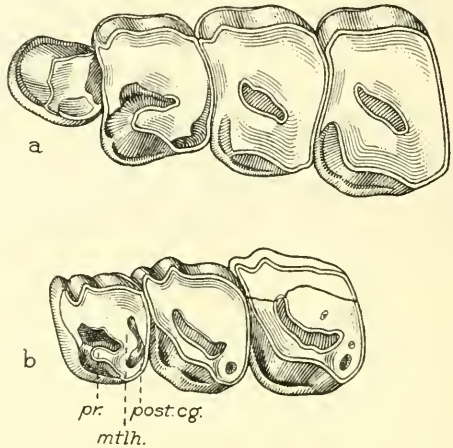

FIG. 11. *a*, *Ancylocoelus frequens* Ameghino. P^{1-4}, F.M. No. P13333. x 1/1. *b*, *Colpodon propinquus* Burmeister. P^{2-4}, F.M. No. P13310. x 1/1. *mtlh.*, metaloph; *post.cg.*, posterior cingulum; *pr.*, protocone.

this element and by a cingulum which arises at the base of its internal slope. On the molars of these two genera the median ridge is not as completely developed as it is in *Leontinia*.

TOXODONTIDAE Gervais

The earlier forms with complex molars (*Nesodon*, *Adinotherium*, etc.), which are referred by some authors to a distinct family, the Nesodontidae, are retained for the present in this family pending further knowledge of the phylogeny of the later forms with simpler molars.

Proadinotherium Ameghino. Fig. 12.

A specimen of *P. muensteri* Ameghino, F.M. No. P13524, with unerupted P^3, P^4, from the Colhué-Huapí beds south of Lake Colhué-Huapí, illustrates the premolar-molar homologies of the earlier members of the family very clearly. The homologies

determined are in full accord with those previously advanced by Simpson (1932, pp. 10–11).

On P^3, P^4 the ectoloph is sinuous, with parastyle and paracone ridges, a prominent convexity at the metacone, and a slight metastyle ridge. On P^3 the protoloph is fully formed; a remnant of the internal half of the anterior cingulum still persists at the base of the enamel at the antero-internal corner of the tooth. The metaloph is attached to the posterior portion of the crescentic protocone. It sends a blunt spur (crochet) anteriorly into the central valley. The posterior cingulum participates in the apical structure but is relatively small. Two cristae extend internally from the ectoloph; the first is large, the second incipient.[1] P^4 is somewhat more molariform than P^3; it is longer antero-posteriorly and more rectangular in outline. The posterior cingulum is situated higher on the posterior face of the tooth and there is a suggestion of a division on the lingual face. The second crista remains small.

On the molars the second crista is large and partially fused with the metaloph. The two isolate a small median external fossette. The crochet abuts against the protocone, isolating a median internal

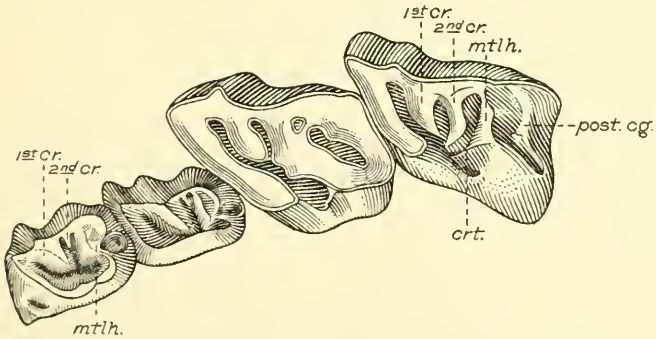

FIG. 12. *Proadinotherium muensteri* Ameghino. P^3–M^2, F.M. No. P13524. x 1/1. *cr.*, crista; *crt.*, crochet; *mtlh.*, metaloph; *post.cg.*, posterior cingulum.

fossette. As in the Leontiniidae, the chief distinction between premolars and molars lies in the lingual fissure separating protocone and pseudohypocone which persists until an advanced stage of wear. The posterior cingulum is situated much higher on the posterior face of the tooth than it is on the premolars; it sends forward a spur into the posterior fossette. Scott (1912, Plate 17, Figs. 2–3)

[1] This second crista, which assumes great prominence on the molars, is not present on the premolars of the Deseado *P. leptognathum*, or, to judge from the figures given by Scott (1912, Plate 17), of the Santa Cruz genera *Nesodon* and *Adinotherium*.

has figured premolars of *Nesodon imbricatus* on which several spurs from the posterior cingulum seem to have reached the metaloph, thus isolating a series of small fossettes in place of the single large posterior fossette.

The homologies of the molars of the later genera are very uncertain. The protoloph remains distinct throughout. In the trilobate molar of *Toxodon* it seems possible that the median lobe could be composed of the combined first and second cristae and the crochet of the *Proadinotherium* molar type, the posterior lobe being made up of the metaloph and posterior cingulum. In the bilobate forms, e.g. *Trigodon*, the posterior lobe could be formed from all the crown elements posterior to the protoloph. These, however, are speculations only; evidence is lacking. I am, nevertheless, inclined to agree with Scott (1912, p. 180) in his belief that the dentitions of these later genera could have been derived from the nesodont type since in *Morphippus* and in the Typotheria examples are found showing tendencies toward secondary simplification of a complex grinding surface.

NOTOHIPPIDAE Ameghino

The forms placed by Loomis in the Rhynchippidae are included in this family for reasons given below (p. 108).

Argyrohippus Ameghino. Fig. 13.

A partial skull of *A. fraterculus* Ameghino, A.M. No. 29685, collected by the Scarritt Patagonian Expedition from the Colhué-Huapí beds to the south of the lake by that name, preserves P^2–M^3

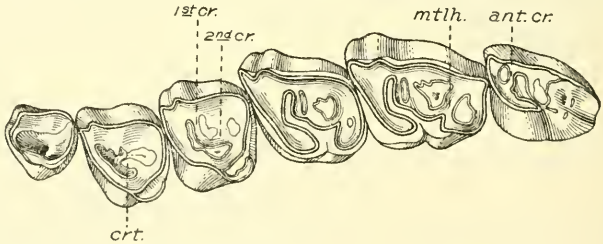

FIG. 13. *Argyrohippus fratereulus* Ameghino. P^2–M^3, A.M. No. 29685. x 1/1. *ant.cr.*, anterior crista; *cr.*, crista; *crt.*, crochet; *mtlh.*, metaloph.

relatively little abraded. This specimen has been previously figured and very briefly described by Simpson (1932, pp. 12–13), with whose homologies the present study is in accord.

P^2 is simple in structure with slight parastyle and strong paracone ridges on the ectoloph and an internal crescent composed of protoloph,

crescentic protocone, and metaloph. There are no clearly defined cristae or crochets and all traces of cingula are lacking. P^3 differs considerably from its predecessor. Three incipient cristae extend internally from the ectoloph; the anterior is very small, the first and second (so-called because they are apparently homologous with the two cristae of the *Proadinotherium* premolar) somewhat larger. A crochet extends anteriorly into the central valley to a point opposite the first crista. There is a cup-like postero-internal cingulum;[1] this structure is lacking on P^2 and its derivation is doubtful. There is some evidence (see below) for considering it as a portion split off from the metaloph rather than a part of the original posterior cingulum. On P^4 both first and second cristae are enlarged and united to the crochet; the tooth is too much worn to show the anterior crista.

The transition from premolars to molars is abrupt in this family yet it appears, as is shown in fig. 13, that the elements of one series,

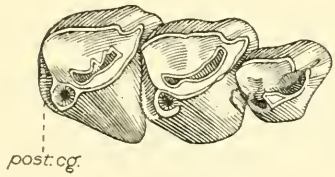

FIG. 14. *Argyrohippus* sp. P^{2-4}, F.M. No. P13334. x 1/1. *post.cg.*, posterior cingulum.

with the possible exception of the protocone, are homologous with those of the other. The anterior crista is very plain on M^3.

The premolars of a specimen of *Argyrohippus* sp., F.M. No. P13334 from the Deseado beds at La Flecha, are of some interest in connection with the question of the derivation of the postero-internal cingulum. P^2 of this form (fig. 14) is more complex than that of *A. fraterculus;* it shows incipient cristae and a ridge extending postero-externally from the protocone. On P^3 this ridge merges with the external half of the metaloph, cutting off the cup-like postero-internal cingulum. In this specimen the external extremity of the cingulum remains connected with the metaloph whereas on *A. fraterculus* it is free for at least part of its height. On P^3 and P^4 of P13334 a portion of the original posterior cingulum is present above the postero-internal cingulum; it therefore seems possible

[1] Ameghino (1904, p. 311, fig. 414) has figured a fourth upper premolar identified as *Proadinotherium leptognathum*. It seems evident from the figure, however, that the specimen is an *Argyrohippus*.

that the latter element is a portion of the metaloph secondarily split off. On P^2 of *A. fraterculus* (fig. 13) there is a slight ridge on the anterior slope of the metaloph which is possibly homologous to the ridge running postero-externally from the protocone on P^2 of P13334. On the molars of the last-mentioned specimen the first crista remains distinct from the crochet in the early stages of wear.

Rhynchippus Ameghino. Fig. 15.

A specimen of *R. pumilus* Ameghino, A.M. No. 29555, from the Deseado beds at Cabeza Blanca, has well-preserved and little-worn premolars and molars. This specimen has been previously

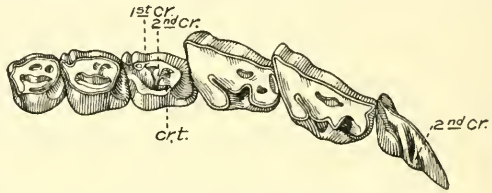

FIG. 15. *Rhynchippus pumilus* Ameghino. P^2–M^2, A.M. No. 29555. x 1/1. *cr.*, crista; *crt.*, crochet.

described and figured by Simpson (1932, pp. 8–12); some of the interpretations given here differ from his.

P^1 is concealed. P^2–^{4} resemble each other closely enough to permit P^4, which is the least worn, to be taken as typical. The general structure having been adequately described by Simpson, it will suffice here to call attention to the details of the central valley. Two cristae (homologous to the first and second cristae of the *Proadinotherium* and *Argyrohippus* premolars) extend internally from the ectoloph; the first crista is joined to the apex of the ectoloph, the second some little distance above the apex. The first crista slopes postero-internally to abut against the inner end of the shorter, transversely directed, second crista. A short crochet also abuts against the extremity of the second crista. With but little abrasion these three structures become indistinguishably fused (as on P^2–^{3}), isolating two shallow external fossettes. Of these the fossette between the second crista and the metaloph is the deeper. Simpson mentioned the fossettes but did not describe the cristae or crochet.

The same author states that there is but one crista on the molars and that it is united to the metaloph, enclosing a single external fossette. On the contrary I am convinced that essentially the same condition prevails on the molars as on the premolars and that the second crista is fused with the first in the early stages of abrasion.

On the unworn M^3, which is only partially erupted, there is a small ridge extending from the first crista to the ectoloph, and united to that crest at some distance above its apex, which seems to represent this structure. The external fossette on M^1, M^2 is here considered homologous to the fossette between the second crista and the metaloph on the premolars.

Suborder ENTELONYCHIA Ameghino. HOMALODOTHERIIDAE Ameghino

Homalodotherium Flower. Fig. 16*a*.

The cheek-teeth are perfectly preserved in the splendid specimen of *H. segoviae* Ameghino, F.M. No. P13092, from the Santa Cruz beds in the vicinity of Cape Fairweather.

The premolars and molars are very similar in structure to those of *Leontinia*. The chief distinction lies in the fact that in *Homalodotherium* the posterior cingulum is relegated to the bases of the molars and takes no important part in the formation of the grinding surface.

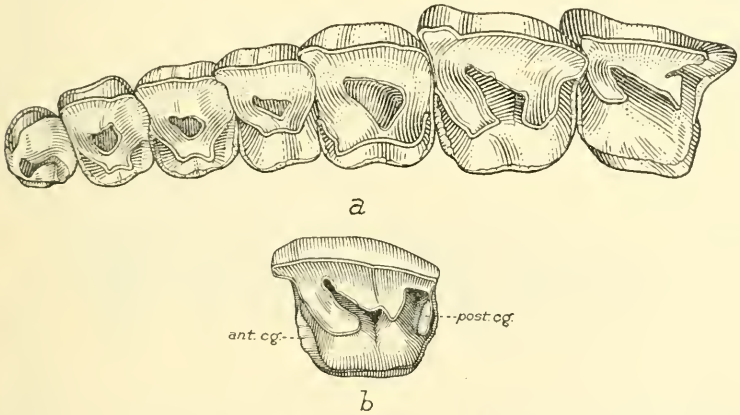

FIG. 16. *a*, *Homalodotherium segoviae* Ameghino. P^1–M^3, F.M. No. P13092. x 1/2. *b*, *Asmodeus* sp. M^2(?), F.M. No. P14711. x 1/2. *ant.cg.*, anterior cingulum; *post.cg.*, posterior cingulum.

In addition the molars in this genus do not have so great an antero-posterior diameter. On P^1 of the specimen figured the protoloph is completely formed but on the corresponding tooth of a specimen of *H. cunninghami* figured by Lydekker (1893, Plate 19, Fig. 1) it is still incomplete. Unworn M^2 and M^3 of *H. segoviae* figured by Scott (1912, p. 253, fig. 43) show several cristae running internally from the ectoloph and a crochet extending anteriorly from the metaloph.

An interesting condition is seen in an upper molar of *Asmodeus* sp., F.M. No. P14711, from the Deseado beds at La Flecha (fig. 16*b*). Fairly large remnants of the original anterior and posterior cingula remain on the corresponding faces of the tooth. Above them, and encircling the entire internal portion of the tooth, is another and very sharply defined cingulum, evidently a secondary development.

ISOTEMNIDAE Ameghino

Pleurostylodon Ameghino. Fig. 17.

A specimen of *P.* (?)*biconus* Ameghino, F.M. No. P13296, from the Casamayor beds south of Lake Colhué-Huapí, exhibits little-worn premolars and molars. The first premolar is a comparatively simple tooth on which the protoloph is not yet formed. P^{2-4} resemble one another fairly closely. On these teeth the ectoloph is very sinuous with strong parastyle and paracone ridges, and the protoloph and metaloph are completely formed. The anterior and posterior cingula are well developed, the posterior situated lower on the crown than the anterior. The central valley is invaded by a varying number of cristae, some of which may have arisen from the ectoloph, others from the floor of the valley; there is no definite and fixed number, such as occurs in the Toxodontidae and Notohippidae.

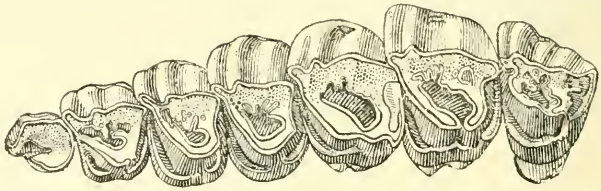

FIG. 17. *Pleurostylodon* (?)*biconus* Ameghino. P^1–M^3, F.M. No. P13296. x 1/1.

A small crochet is present. There is no indication of a division on the lingual face.

Essentially the same pattern is characteristic of the molars. On M^1, M^2 the pseudohypocone is separated from the protoloph but the division is not deep and is soon effaced by abrasion. On M^3, as in the Leontiniidae and Homalodotheriidae, the division is not apparent. The posterior cingulum is better developed than it is in *Homalodotherium* and *Asmodeus* and participates to a slight extent in the formation of the grinding surface. On M^3 the postero-internal portion of the cingulum is elevated, forming a very indistinct and incipient hypocone.

Suborder TYPOTHERIA Zittel

Very few specimens of the Deseado and later typotheres are known which show the crown pattern of premolars and molars. The reason for this is that the members of this suborder early tended toward the development of a flat grinding surface and the consequent elimination of details of crown structure. Sinclair (1909, p. 8) has figured an unworn M^3 of *Protypotherium*, and specimens of *Trachytherus* and of *Prosotherium* are described below. The majority of the Casamayor typotheres figured by Ameghino show cristae and crochets similar in general to those of the Notohippidae and the earlier Toxodontidae. The genus *Notopithecus* (=*Adpithecus*), now known to be an interatherid (Riggs and Patterson), has a united crista and crochet in the median valley.

TYPOTHERIIDAE Lydekker

Trachytherus Ameghino. Fig. 18.

The position of this genus has been very uncertain hitherto. Study of an excellent series from the Deseado beds at Cabeza Blanca and La Flecha has convinced me that it is an ancestral typotherid and should be placed in the Typotheriidae. A preliminary description and discussion of these specimens appears in another paper of this series. A specimen from Cabeza Blanca, A.M. No. 29564, preserves dm^3–M^2. The crowns of P^3–^{4} were lying beneath the milk molars and these have been skilfully removed by Mr. J. B. Abbott without injury to the specimen.

Both premolars are quadrangular in outline; the metaloph on each slopes rapidly inwards at the apex, thus causing the central valley to be considerably smaller than it would be on a slightly abraded tooth. There is no trace of an anterior cingulum; the posterior cingulum is large and is joined to the internal slope of the protocone. Protoloph and metaloph are complete; the protoloph is cuspidate immediately external to its junction with the protocone, the cusp being incipient on P^3 and prominent on P^4. In some specimens of this species, e.g. the one figured by Loomis (1914, p. 81, fig. 48), the protoloph evidently remains distinct from the protocone until a fairly advanced stage of abrasion is reached. A short, thick crista extends internally from the ectoloph on both teeth. On P^4 the crista is met by a long and stout crochet from the internal end of the metaloph, a structure which is lacking on P^3. The transition from premolars to molars is very sharp.

The molars are long antero-posteriorly and narrow transversally, on eruption. Each is composed of three approximately subequal lobes extending internally from the gently convex ectoloph. As abrasion proceeds the median lobe decreases in size and finally disappears entirely. According to the evidence of the premolars, and of the molars of interatherids such as *Notopithecus*, this element is very probably formed from a combined crista and crochet, but the homologies of the anterior (protoloph) and posterior (metaloph + posterior cingulum) lobes are extremely uncertain. It cannot be determined from the material at hand whether or not the protocone has undergone division. If it has been divided, then a portion of it is included in the anterior lobe, but if the contrary is the case it is restricted to the posterior lobe. The conditions in the premolars of *Trachytherus* and certain other typotheres (see below) would indicate that there has been no division of the protocone and that

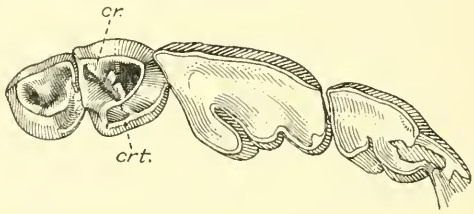

FIG. 18. *Trachytherus spegazzinianus* Ameghino. P^2–M^2, A.M. No. 29564. x 1/1. *cr.*, crista; *crt.*, crochet.

the protoloph (protoconule) has grown inward to occupy the antero-internal corners of the teeth. Premolar analogy, however, may not be a safe guide in this case since there is no evidence that premolars and molars have undergone exactly the same developmental history. Some of the Casamayor typotheres figured by Ameghino (1904) have molars with a continuous internal face which could be taken as indicating that division probably took place in the later forms. In the absence of connected phylogenetic series it is impossible to settle this question.

HEGETOTHERIIDAE Ameghino

Prosotherium Ameghino. Fig. 19.

A specimen of this genus, A.M. No. 29556, from Cabeza Blanca shows the crown patterns of P^2–M^2 very satisfactorily. P^2 is a simple tooth with a convex ectoloph and a stout postero-internal protocone connected to the posterior portion of the ectoloph.

There is no trace of an anterior cingulum on any of the teeth of the specimen; the posterior cingulum isolates a small fossette on all of them. P^3 and P^4 are identical in appearance and much more complicated than P^2. The parastyle is large and separated by a wide, shallow groove from the prominent paracone. The protoloph (protoconule) extends postero-internally from the parastyle and abuts against the protocone but does not unite with it until abrasion

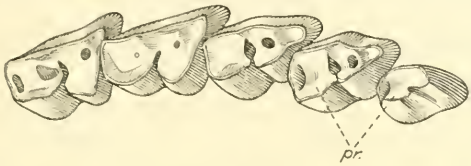

FIG. 19. *Prosotherium* sp. P^2–M^2, A.M. No. 29556. x 2/1. *pr.*, protocone.

has proceeded for some time. A stout crista (possibly crista plus antecrochet) joins the ectoloph to the protoloph, isolating an antero-external fossette. A second crista connects the ectoloph with a spur extending anteriorly from the internal extremity of the metaloph; there are no united cristae and crochets such as are present in *Notopithecus* and other interatherids. On the molars the protolophs are somewhat larger, the lingual divisions are persistent, and the ectolophs gently concave. In other respects the structure is identical with that of the premolars. The protolophs of both series may be homologous but, as stated in the preceding section, there is no definite evidence that they are.

Suborder NOTIOPROGONIA Simpson.[1] ARCTOSTYLOPIDAE Schlosser

Palaeostylops Matthew and Granger. Fig. 20.

Matthew and Granger (1925) and Matthew, Granger, and Simpson (1929) have described and figured two species of this peculiar genus from the Gashato Paleocene of Mongolia. From a study of a specimen determined as *P. iturus* Matthew and Granger, F.M. No. P14125, and from the figures and descriptions given by the authors cited it is possible to arrive at tentative homologies.

On the premolars the ectoloph is high and straight; there is some indication on P^1 and P^2 of P14125 that it is composed of three subequal elements, presumably parastyle, paracone, and metacone. According to Matthew, Granger, and Simpson (1929, p. 12) the internal cusp, sharply defined on P^4, begins as a slight internal

[1] For definition and discussion of this new suborder see Simpson, 1934, pp. 10–16.

heel on I^1 and becomes progressively stronger on the succeeding teeth. This internal cusp may be regarded as the "protocone." Protoloph and metaloph are very poorly defined and there appear to be no cingula. The transition from premolars to molars is more abrupt in this genus than in any other which I have observed.

The molars present several very interesting features. The prominent antero-external pillar on the ectoloph described by Matthew and Granger is probably the parastyle. The separation of protoloph and pseudohypocone is partial on M^1, very complete on M^2 and apparently lacking on M^3. Matthew and Granger state that the metaloph extends transversely inwards from the middle of the ectoloph and apparently sends a wing postero-externally, but

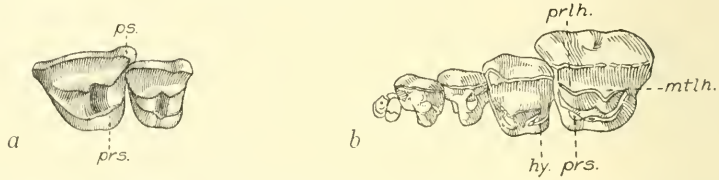

FIG. 20. *a*, *Palaeostylops iturus* Matthew and Granger. M^{1-2}, F.M. No. P14125. x 3/1. *b*, *Palaeostylops macrodon* Matthew, Granger, and Simpson. x 3/1. Redrawn after Matthew, Granger, and Simpson. Lettering original. *hy.*, hypocone; *mtlh.*, metaloph; *prlh.*, protoloph; *prs.*, protostyle; *ps.*, parastyle.

it can be assumed with equal probability that it extended antero-internally from the posterior part of the ectoloph. Apparently no specimen shows the central valley, so that it is impossible to state whether or not accessory cuspules were present. The cingula of M^1 and M^2 show the most interesting features of the molar series; to judge from the available figures, M^3, which most nearly resembles the premolars, does not have cingula developed to any appreciable extent. On M^1 of P14125 there is a cingulum encircling the internal face of the tooth, on the specimens figured by the authors cited above the anterior and posterior cingula do not meet; on M^2 of P14125 and the figured material there is a continuous internal cingulum. The figured specimens of *P. macrodon* Matthew, Granger, and Simpson and P14125 have the metaloph shorter than the protoloph on M^1, conversely on M^2. Possibly in correlation with the respective lengths of the lophs, there is a tendency, incipient in P14125 but well marked in *P. macrodon*, to develop a cingulum hypocone on M^1 and a protostyle on M^2. One of the specimens of *P. macrodon* (fig. 20*b*) shows a second cingulum cusp on M^2 behind the protostyle.

The evolutionary tendency in this family possibly may have lain in the direction of loph reduction and the development of cingulum cusps as a compensatory feature. There is no evidence of any such tendency in the South American families of the order. The Isotemnidae perhaps approach the closest in development of the cingula—the very incipient hypocone on M^3 of *Pleurostylodon*, mentioned above, is noteworthy in this connection—but there is no indication of reduction in the lengths of the lophs.

NOTOSTYLOPIDAE Ameghino

Notostylops Ameghino. Fig. 21.

The description has been taken from several specimens from the Casamayor beds belonging to various species.

The premolars and molars resemble each other closely. The ectolophs of both series are moderately sinuous, with rounded parastyle and paracone ridges; the latter are somewhat more prominent on the premolars than on the molars. The protocone is crescentic on the premolars; there is an incipient division of the lingual face of M^1 and M^2 but not of M^3. The protoloph is not united to the ectoloph until a fairly advanced stage of abrasion is reached. The metaloph is connected somewhat earlier; on P^4 of P14720 this crest is cuspidate near its junction with the ectoloph (fig. 21). The

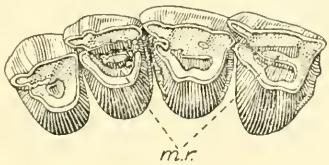

FIG. 21. *Notostylops* sp. P^3–M^3, F.M. No. P14720. x 3/2. *m.r.*, median ridge.

anterior and posterior cingula are weak throughout and lacking entirely on some premolars. The central valley is invaded by a long spur from the metaloph which is separate from the ectoloph in the early wear stages. This spur has been formed by cuspules arising in the valley and coalescing with each other and with the metaloph (P^4, fig. 21).

MILK MOLARS

Specimens that are sufficiently young to show structural details of the deciduous dentition are very rare in the collections at hand. There is, however, one specimen of *Leontinia*, F.M. No. P14659, from the Deseado beds at Cabeza Blanca which shows

interesting transitions in the structure of the lingual face between dm^2 and dm^4 (fig. 22).

On dm^2 the protocone is stout and postero-internal in position. The metaloph is complete and the posterior cingulum, although small, participates in the structure of the crown. The protoconule is large and elongate transversely. On dm^3 the protoconule is greatly enlarged and is equal in size to the protocone, with which cusp it is fused for most of its height. Dm^4, with its large L-shaped protoloph and small pseudohypocone, is an exact replica of the permanent first and second molars.[1] To judge from these teeth the development of the milk molars is as follows: The protocone is postero-internal in position; the protoconule becomes progressively larger, forming a protoloph which then fuses with the protocone to build a lingual wall; division of this wall subsequently ensues. The pseudohypocone of dm^4, and hence probably of the molars also,[2] is, therefore, a portion of the protocone which is in its original position, while the protoloph is composed chiefly of the protoconule supplemented by a portion

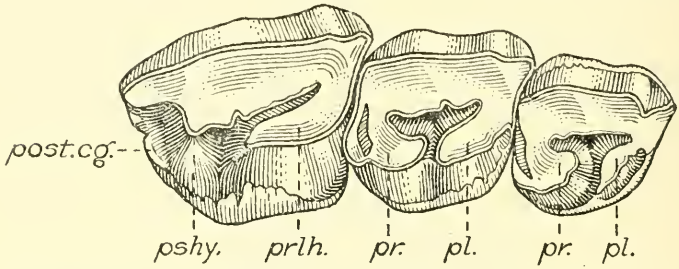

FIG. 22. *Leontinia gaudryi* Ameghino. Dm^2–dm^4, F.M. No. P14659. x 1/1. *pl.*, protoconule; *post.cg.*, posterior cingulum; *pr.*, protocone; *prlh.*, protoloph; *pshy.*, pseudohypocone.

of the protocone slightly removed from its original position. The development of milk molars of this genus differs somewhat from that of the premolars described above. In the teeth of the latter series the protocone is central in position and the protoconule (or rather, the ridges occupying the position of this cusp) does not form an independent protoloph but becomes connected to the protocone at an early stage.

[1] On M^2 of *Leontinia*, *Homalodotherium*, and other genera there has been no division and the combined protocone-protoconule extends across the entire lingual face.

[2] Although the protocone of the milk molars may not be strictly homologous in origin to the protocone of the molars, the two cusps are obviously homologous in function. It seems probable, therefore, that after the "protocone" of the milk molars came into use it underwent division in the same manner as the protocone of the molars.

A point that must be considered here is the possibility that dm^4 and the molars have developed differently from dm^{2-3}. The protocone on this tooth may have been antero-internal in position instead of postero-internal and the metaconule may have expanded inwardly as in the Eocene horses described by Granger (1908, pp. 260–262). In this case no division of the lingual face would have taken place. The structure of the roots, however, is against such a supposition. On dm^2 there is a single stout internal root which is mainly beneath the protocone; on dm^3 this root sends a spur antero-externally beneath the enlarged protoconule. On dm^4 this spur is greatly enlarged but the portion of the root beneath the pseudohypocone is still slightly thicker. The same condition may be noted in the internal root of the permanent molar of *Asmodeus* sp. figured above. If the postero-internal cusp represents an enlargement of the metaconule it is logical to assume that the portion of the root beneath it would be considerably smaller than the part beneath the protoloph.[1]

The milk molars of *Nesodon* and *Adinotherium* figured by Scott (1912, Plate 17, Figs. 1, 8) appear to indicate a development similar to that of *Leontinia*. Development in other toxodont and entelonychian families may be the same but evidence is not available at present. Conditions in the Typotheria are very uncertain. A specimen of *Plagiarthrus* (=*Argyrohyrax*) shows essentially the same milk molar structure and development of the protoloph as that shown by the premolars of *Prosotherium* described above.

SUMMARY

The ancestral notoungulates undoubtedly possessed simple, trigonal upper molars; there was probably some degree of regional anisomerism between these teeth and the upper premolars. Limited secondary polyisomerism in the cheek-teeth later arose through the development of cristae and crochets, but in relatively few cases did the premolars of the later notoungulates become completely molariform.

The tendency for cuspules to arise from the floor of the median valley and from the internal slopes of the ectoloph and metaloph is an ordinal character of the Notoungulata. The developments attained by these cuspules on the molars of the later members of the various families are highly characteristic.

[1] Dr. Granger has very kindly informed me (letter of February 15, 1934) that in *Orohippus* (in which the protocone is antero-internal on P^4 and postero-internal on P^3) the antero-internal root is larger than the postero-internal on P^4 and smaller on P^3.

In the Leontiniidae (especially *Leontinia*) a massive, papillate ridge is formed which extends anteriorly from the metaloph.

In the earlier Toxodontidae two prominent cristae extend internally from the ectoloph, the posterior uniting with the metaloph. A crochet is also formed.

In the Notohippidae two main cristae are present; in some genera these unite with a crochet.

In the Homalodotheriidae and Isotemnidae a crochet and a variable number of cristae occur.

In the Typotheriidae the combined crista and crochet probably form the prominent median lobe.

In the Interatheriidae an antecrochet was probably present in addition to a combined crista and crochet.

In the Hegetotheriidae two cristae connect the ectoloph to the protoloph and to a spur extending anteriorly from the internal extremity of the metaloph. As far as known, there is no united crista and crochet.

The holarctic Arctostylopidae possibly represent a trend toward the reduction of the lophs and the development of cingulum cusps.

In the Notostylopidae a simple ridge is developed which extends anteriorly from the metaloph.

The postero-internal cusp of the upper molars of the Toxodonta and Entelonychia appears to be a pseudohypocone; in the Typotheria it is uncertain whether this cusp is a pseudohypocone or the protocone.

NOTES ON TAXONOMY

LEONTINIIDAE.—The subordinal position of this family is uncertain. In dental characters the leontiniids resemble the Entelonychia rather more than they do the Toxodontidae and Notohippidae. The affinities of the family, based on a study of *Leontinia*, *Colpodon*, and *Ancylocoelus*, will be discussed in a paper now in preparation.

NOTOHIPPIDAE.—If the homologies of the premolars and molars of this group given on page 98 are correct, which I believe to be the case, then the validity of the Rhynchippidae is highly questionable. This family was erected by Loomis (1914, pp. 87–89) for the genera *Rhynchippus*, *Morphippus* and *Eurygenium*.[1] This author stated that in his opinion the Notohippidae should be suppressed

[1] *Eurygenium* Ameghino (1895, p. 655), later changed to *Eurygeniops* by the same author (1897, p. 464). According to the International Rules the change is not justified, *Eurygenium* not being preoccupied by *Eurygenius* Laferté.

since *Notohippus* was so little known and since most of the genera referred by Ameghino to this family (*Coresodon*, *Interhippus*, *Stilhippus*, *Nesohippus*) should be placed in the Nesodontidae. This disposition of these forms is in my opinion unjustified, since all of them have cement on the teeth (fide Ameghino), a character typical of many notohippids but totally lacking in the Toxodontidae (in which the "Nesodontidae" are here included). The Notohippidae may be regarded as a valid family closely resembling the earlier members of the Toxodontidae in upper molar structure. There now remains the question of the validity of the Rhynchippidae. Loomis distinguished this group on the basis of (1) brachyodont, or nearly brachyodont, molars, and (2) the absence of cristae. *Rhynchippus* is no more brachyodont than the contemporary *Argyrohippus* sp. mentioned above, which disposes of (1); (2) is shown to be incorrect by the American Museum specimen. Simpson (1932) recognized both Notohippidae and Rhynchippidae, distinguishing the latter by (*a*) the presence of one crista only on the molars, and (*b*) the absence of cement. In regard to (*a*) the interpretation of the *Rhynchippus* molar given above is at variance with that proposed by Simpson; if correct it disposes of this argument. In any event the upper premolars of *Rhynchippus* and *Argyrohippus* are in fairly close agreement and differ from those of the early toxodontids in the possession of relatively well-developed second cristae. Point (*b*) cannot be considered as a criterion for the distinction of the two groups, for Ameghino (1904, p. 222) states that cement occurs in *Rhynchippus* and *Morphippus*. It does not occur universally on specimens of these genera but the writer has detected it on certain lower molars of *Morphippus* in the Field Museum collections. The distribution of cement in members of this family presents analogies to conditions observed in the Miocene Equidae.

In conclusion, therefore, I do not recognize the Rhynchippidae as a valid family distinct from the Notohippidae. A fundamental character common to all the genera sufficiently well known to show it, and employed by Ameghino in his definition of the family (1895, p. 630), is the arrangement and structure of the incisors. These teeth are approximately subequal and are grouped in a semicircle around the muzzle; a similarity of structure is apparent in all the genera in which they are known. The possibility that there may be divergent lines of development within the limits of the Notohippidae, which may in the future be recognizable as subfamilies, is not excluded, but the evidence at present available is far too scanty to

attempt such groupings. *Rhynchippus* and *Morphippus*, however, do seem to represent a trend towards the elimination of details of crown pattern and the development of a flat, featureless grinding surface such as occurs in the later typotheres and toxodontids. Loomis (1914, p. 105) considers this condition in *Morphippus* as primitive, a view to which I cannot subscribe.

ASTRAPOTHERIA.—Any extended discussion of the dentition of this group is out of place here but a brief note may be appended. The molars of the later astrapotheres, *Parastrapotherium* and *Astrapotherium*, resemble those of certain notoungulates closely, as they possess large L-shaped protolophs and prominent cristae and crochets. This resemblance has led the majority of authors to place them in the Notoungulata. The astrapothere protocone, however, is antero-internal in position on both premolars and molars and the protoloph on the premolars is formed before the metaloph. The postero-internal cusp of the molars appears to be a cingulum hypocone. These features are certainly not typical of the majority of notoungulates. Similarity in molar structure is the only claim of the Astrapotheria to inclusion in the Notoungulata, and the similarity seems to be more analogous than truly homologous. I therefore abandon my previous classification (1932), in which the order Notoungulata was divided into two suborders, Toxodontia and Astrapotheria, and regard the astrapotheres as a distinct order, following Scott (1928) and Simpson (1933, 1934).

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